

THE COMPARATIVE MORPHOLOGY OF THE WINTERACEAE I. POLLEN AND STAMENS

I. W. BAILEY AND CHARLOTTE G. NAST

With three plates

INTRODUCTION

THE genera *Drimys*, *Pseudowintera*, *Belliolum*, *Bubbia*, *Exospermum*, *Zygogynum*, *Tetracentron*, and *Trochodendron* are the only known living representatives of the dicotyledons that have retained a primitive vesselless type of secondary xylem. In fact, it was upon the basis of their exceptional wood structure that van Tieghem (6) segregated them in three families of a distinct order, the Homoxylées. *Tetracentron* and *Trochodendron* are monotypic, whereas the six winteraceous genera are now represented by approximately 88 species. Thus, the Winteraceae may no longer be regarded as a few bizarre relics, since they are a flourishing family, having representatives in Mexico, Central and South America, New Zealand, Australia, New Caledonia, New Guinea, the Solomons, the Philippines, and adjacent regions.

There has been much uncertainty in the past concerning the relationships and the morphological significance of the Winteraceae. Now that much new material has been accumulated, it seems desirable to institute a detailed re-investigation of the family. Our colleague, Dr. A. C. Smith (4, 5), has published two extensive taxonomic revisions of the family. In so doing, he assembled a large amount of material from American herbaria, which has provided us, in turn, with a wide range of accurately determined specimens, upon which to base a comprehensive study of the comparative morphology of the flowers, leaves, and stems of the Winteraceae. The first paper of our series deals with the pollen and stamens of the family. The succeeding paper will discuss the remarkable carpels of the Winteraceae, which rival their vesselless wood in morphological significance. The herbarium specimens upon which our studies are based have been listed in Dr. Smith's papers and need not be relisted here.

POLLEN

Wodehouse (7, 8) has advanced the intriguing hypothesis that there are two basically different types of pollen morphology. The single-grooved or *monocolpate* type (variously modified by phylogenetic changes) characterizes the gymnosperms from the Bennettitales to the Coniferales and is of common occurrence in monocotyledons, but is confined among dicotyledons to certain representatives of the Ranales. On the contrary, the 3-grooved or *tricolpate* type (and its derived forms) is characteristic of most dicotyledons. In recent comprehensive surveys of the pollen of

various dicotyledonous families, we have accumulated considerable evidence in support of certain aspects of this hypothesis. It is evident, for example, that plants of ranalian affinities may be divided upon the basis of their pollen morphology into two distinct categories:

I. WITH MONOCOLPATE OR DERIVED TYPES OF POLLEN

Winteraceae	Annonaceae	Hernandiaceae	Lactoridaceae
Degeneriaceae	Myristicaceae	<i>Austrobaileya</i>	Piperaceae
Magnoliaceae	Monimiaceae	Canellaceae	Saururaceae
Himantandraceae	Lauraceae	Calycanthaceae	Cabomboideae
Eupomatiaceae	Gomortegaceae	Chloranthaceae	Nymphaeoidae

II. WITH TRICOLPATE OR DERIVED TYPES OF POLLEN

Schizandraceae	Trochodendraceae	Ranunculaceae	Menispermaceae
<i>Illicium</i>	Eupteleaceae	Lardizabalaceae	Nelumbonoideae
	<i>Tetracentron</i>	Berberidaceae	

All of the plants in the first category, with the exception of the aquatic Cabomboideae and Nymphaeoidae, have secretory cells of the well known ranalian type. In the second category, such cells occur in the Schizandraceae, *Illicium*, and *Tetracentron* only.

Wodehouse (7) homologizes the monocolpate pollen of angiosperms with similar one-furrowed pollen of the lower gymnosperms. In so doing, he assumes that the single germinal furrow is on the distal face of the pollen grains, i.e. the exposed outer surface of the pollen grains during the tetrad stage of development. The pollen of the Winteraceae is shed in tetrahedral tetrads, *Figs. 1-13*, and each of the four grains is provided with a circular germ pore in its distal (outer) face. Wodehouse interprets the pollen of *Drimys* as of a modified monocolpate type, and infers from this that the single germinal furrow of other ranalian plants is on the distal face of the grains. It is significant in this connection, however, that one of our co-workers, Mr. S. J. Golub, finds that the pollen of the Annonaceae not infrequently tends to be more or less coherent in tetragonal tetrads at the time of shedding. These tetrads, *Fig. 14*, demonstrate that the germinal furrow of annonaceous pollen, *Fig. 15*, is on the proximal (inner) face of the pollen grains; this raises the question whether such is not likewise the case in the Myristicaceae, Magnoliaceae, and other related ranalian families. The tetrads of the Winteraceae are firmly coherent, and only in one instance (*Drimys brasiliensis* var. *campestris* (St. Hil.) Miers, *Hoehne 28700*) have we encountered a few dissociated tetrads. As indicated in *Fig. 13*, the isolated pollen grains have, in addition to the distally located circular germ pore, proximal facets that closely resemble those of annonaceous pollen, compare *Figs. 13* and *15*. In other words, it cannot be assumed *a priori* that the distal germ pore of *Drimys* developed by a simple reduction in the size of the germinal furrow of Magnoliaceae, since the germinal furrow of annonaceous pollen is not a direct homologue of the distally oriented circular germ pore of winteraceous pollen, but rather of its unthickened proximal facets, compare *Figs. 12, 13* with *Figs. 14, 15*.

The morphological specializations of monocolpate types of pollen are numerous and diverse, apparently leading to the formation of dicolpate

(Calycanthaceae, Monimiaceae, monocotyledons), belted (Monimiaceae, Eupomatiaceae, Nymphaeaceae, monocotyledons), polycolpate (Chloranthaceae, monocotyledons), and acolpate (Chloranthaceae, Monimiaceae, Lauraceae, Hernandiaceae, monocotyledons) types. Such phylogenetic trends in the specialization of angiospermic pollen can be clarified only by intensive investigations of a wide range of Ranales and monocotyledons. Furthermore, it is essential to determine the effects of contacts not only within tetrads, but also within groups of contiguous tetrads.

In the case of the Winteraceae, the problems of phylogeny are complicated by the fact that the pollen of all investigated genera and species is shed in permanent tetrads. Since the structure of the individual grains of such tetrads frequently is much modified through excessive specialization, there are no reliable means of determining what the morphological characteristics of the ancestral free grains may have been. Nor is it possible to solve the difficulty by comparisons with the permanent tetrads of Lactoridaceae, *Hedycarya* (Monimiaceae), or *Victoria* (Nymphaeaceae), for in these tetrads specialization has progressed along different lines. The tetrads of the Winteraceae are morphologically unique among plants of ranalian affinities and cannot justifiably be cited as evidence of closer relationship to the Magnoliaceae than to other ranalian families.

The most comprehensive previous investigation of the pollen of the Winteraceae is that of van Tieghem (6), who studied representatives of all six genera of the family. Although providing no illustrations or detailed descriptions of the pollen, he noted certain significant morphological differences within the family. Thus, he emphasized the fact that the pollen of *Drimys Winteri*, *D. brasiliensis*, and *D. granadensis* forms protuberant papillae when moistened, whereas that of *D. membranacea*, *D. piperita*, *Pseudowintera*,¹ *Bubbia*, *Belliolum*, *Exospermum*, and *Zygogynum* does not. In addition, he states that the pollen of *Belliolum*, *Exospermum*, and *Zygogynum* has a granular exine, whereas that of *Drimys*, *Pseudowintera*, and *Bubbia* exhibits a verrucose sculpture.

Our own investigations of numerous species of the genus *Drimys* indicate that in general the tetrads of the Old World Section (*Tasmannia*), Figs. 2-5, are conspicuously smaller than the tetrads of the New World Section (*Wintera*) of the genus, Fig. 1. In the case of Sect. *Tasmannia*, Figs. 2, 3, and 5, as in *Pseudowintera*, *Bubbia*, *Belliolum*, *Exospermum*, and *Zygogynum*, the entire floor of the circular pore bulges outward more or less uniformly during re-expansion of the pollen, whereas in Sect. *Wintera* the central part of this floor bulges rapidly and precociously, leaving a constricting rim or collar of presumably thicker or less elastic material, Figs. 1, 12, and 13. The individual pollen grains of *Drimys*, Figs. 1-5, 9, 11, and 13, *Pseudowintera*, Fig. 8, and *Bubbia*, Fig. 7, are provided (between their distal germ pore and their adnate proximal facets) with a broad zone or belt, Fig. 13, of coarsely reticulate thickening, whereas those of *Exospermum* and *Zygogynum*, Figs. 6 and 10, have minutely re-

¹*Pseudowintera* Dandy, i. e. *Wintera* sensu v. Tiegh., non Murray.

ticulate thickening. The pollen of *Belliolum crassifolium* (Baill.) v. Tiegh., *B. haplopus* (Burtt) A. C. Sm., Fig. 11, and *B. Burttianum* A. C. Sm. is coarsely reticulate and resembles that of the former category of genera. Therefore, we are unable to follow van Tieghem (6) in describing the pollen of *Belliolum* as granular rather than as verrucose. Since he provides no illustrations or detailed descriptions, it is difficult to determine just what he had in mind in using the unqualified general terms "verruqueuse" and "granuleuse". The more or less conspicuously buttressed reticulate thickenings, Figs. 1-5, 7-9, 11, and 13, of the tetrads of *Drimys*, *Pseudowintera*, *Bubbia*, and *Belliolum* are composed of rows of more or less coalesced rods, appearing linear or granular at different focal levels, Fig. 16. Furthermore, the reticulate thickening appears more or less granular in surface view, depending upon the degree of coalescence in its constituent rods and upon the amount of buttressing. In certain species of *Bubbia*, e.g. *B. Clemensiae* A. C. Sm., *B. longifolia* A. C. Sm., and *B. monocarpa* A. C. Sm., Fig. 16, the pollen has a finer mesh of more numerous, slender, partly coalesced rods. The reticulate thickenings of such tetrads are conspicuously granular appearing at lower focal levels. Similarly, in the case of *Exospermum* and *Zygogynum*, the exine appears finely reticulate, Fig. 10, or minutely granular, Fig. 6, at different focal levels. There is, however, in the material that we have studied, a wide structural gap between the minutely granular-reticulate exines of *Exospermum* and *Zygogynum* and the coarsely granular-reticulate exines of the other four genera of the Winteraceae.

There are families of dicotyledons in which the pollen is of very considerable taxonomic significance, not only in the differentiation of subfamilies and tribes, but also of genera and species. Our investigations of numerous collections of all four species of the New World Section (*Wintera*) of *Drimys* and of ten of the thirteen taxonomic entities recognized by Smith (4) indicate that, although the pollen of these plants may be easily differentiated from that of other representatives of the family, it is difficult to distinguish species and varieties within the Section *Wintera*. In the case of the Old World Section (*Tasmannia*) of *Drimys*, *Pseudowintera*, *Belliolum*, and *Bubbia*, the size and form of the tetrads, Figs. 2-5, the diameter of the germ pore, Figs. 9 and 11, the distribution of wart-like thickenings on the floor of the germ pore, Figs. 9, 11, and 16, the detailed structure of the reticulate thickenings, Figs. 9, 11, and 16, and other characters fluctuate more or less from species to species. More material must be examined, however, before attempting to construct a key for differentiating species and genera. Our investigations do suggest that the pollen of Sect. *Wintera* of *Drimys*, on the one hand, and of *Exospermum* and *Zygogynum*, on the other hand, represent two stabilized specializations from the more varied and generalized types of pollen encountered in *Belliolum*, *Bubbia*, *Pseudowintera*, and Sect. *Tasmannia* of *Drimys*.

STAMENS

In the Degeneriaceae (Bailey and Smith 1) and the Himantandraceae

(Diels 3, Bailey, Nast, and Smith 2), the stamens are not differentiated into filament, anther, and connective, but are essentially 3-veined microsporophylls of comparatively unmodified form. The two pairs of slender, vertically elongated sporangia are immersed beneath the abaxial surface of the sporophylls. They are situated between the median and lateral veins, and neither these veins nor their branches are directed toward the sporangia. Thus, the narrow shields of endothecia are not in contact with vascular tissue. Dehiscence is longitudinal and extrorse. The closely allied Magnoliaceae exhibit various modifications of such primitive 3-veined microsporophylls, leading to the formation of more typical stamineal organs. The much enlarged, conspicuously protuberant, paired sporangia (thecae) are lateral on a much constricted part (connective) above the broad base (filament) of the microsporophyll. The thecae may be turned slightly outward or inward, and the longitudinal dehiscence, therefore, fluctuates between extrorse and introrse. In certain representatives of the family, the lateral veins of the modified microsporophylls are much reduced and may at times be eliminated, leaving a single-veined stamen, such as characterizes so many of the dicotyledons.

Although the stamens of the Winteraceae vary considerably in external form, *Figs. 17–24*, they are throughout the family of the single, dorsally-veined type. Four of the genera, *Bubbia*, *Fig. 22*, *Pseudowintera*, *Fig. 23*, *Exospermum*, *Fig. 24*, and *Zygogynum* have short, comparatively broad, more or less truncated and apically flaring microsporophylls. The protuberant sporangia are attached to the broad apex of these sporophylls and are oriented either at right angles to the dorsal vein, *Figs. 22 and 23*, or in various diagonal positions, *Fig. 24*. Dehiscence is, therefore, apical and transverse or obliquely apical. On the contrary, the stamens of *Belliolum*, *Fig. 21*, are generically characterized by their more elongate form and particularly by having their laterally attached sporangia oriented parallel to the long axis of the sporophyll. Dehiscence is longitudinal and more or less conspicuously extrorse.

The microsporophylls of these five genera of the Winteraceae have no constricted part that may be designated as connective, and the sporangia are not excessively protuberant beyond the outlines of the sporophylls. The stamen illustrated in *Fig. 21* resembles in form the microsporophylls of *Himantandra* and *Austrobaileya*. It differs from those of the former genus in its more protuberant sporangia and in having no lateral veins, from those of the latter genus in its unbranched median vein, which does not extend beyond the level of the sporangia. In such species of *Belliolum* as *B. crassifolium* (Baill.) v. Tiegh. and *B. Burtianum* A. C. Sm. the unvascularized upper part of the sporophyll is considerably reduced in length. This suggests that the types of stamens illustrated in *Figs. 22–24* may have developed phylogenetically by elimination of this part of the microsporophyll, with concomitant shifting of the sporangia from longitudinal lateral orientations to obliquely apical and transversely apical ones.

The microsporophylls of *Drimys*, *Figs. 17–20*, fluctuate considerably in length, not only in different species, but also within the same flower. They

are characterized, however, by having markedly protuberant thecae that are attached to the much constricted upper part of the sporophyll. The subapical thecae are oriented parallel to the long axis of the sporophyll or at acute angles to it. Dehiscence is, therefore, approximately longitudinal-lateral and more or less conspicuously extrorse. The microsporophylls of the New World Section (*Wintera*) of the genus are relatively broad, *Figs. 17-19*, but those of the Old World Section (*Tasmannia*) occasionally are much elongated and narrow, *Fig. 20*. The latter are more typically staminal, obviously exhibiting differentiation into filament, connective, and anther.

The median (dorsal) vein of winteraceous stamens may extend throughout the sporophyll without branching, *Figs. 18, 21, 22, and 24*, or it may give off one, *Fig. 19*, or more, *Figs. 17, 20, and 23*, short branches that are directed toward the thecae. Branching of the dorsal vein is in general more extensive and conspicuous and occurs at a lower level in *Pseudowintera* and certain species of *Bubbia*, e.g. *B. pachyantha* A. C. Sm., than in other representatives of the Winteraceae. Spherical secretory cells, *Fig. 18*, are of common occurrence in the microsporophyll, as in other organs, of the Winteraceae. Their contents usually are dissolved during the clearing and mounting of the stamens and, therefore, are invisible in most figures of Plate III. The coriaceous floral appendages of certain species of *Bubbia*, *Exospermum*, and *Zygogynum* contain very numerous sclereids or clusters of sclereids. As indicated in *Fig. 24*, the stamens of such flowers may contain more or less numerous sclerenchymatous cells.

It should be emphasized in conclusion that there appear to be two distinct trends of specialization in the microsporophylls of the Winteraceae, leading in *Pseudowintera*, *Bubbia*, *Exospermum*, and *Zygogynum* to the formation of broadly truncated sporophylls bearing transversely oriented apical sporangia, and in *Drimys* to apically constricted sporophylls bearing laterally attached subapical sporangia.

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EXPLANATION OF PLATES

PLATE I

Unstained tetrads mounted in lactic acid and photographed at a magnification of 1180. FIG. 1. *Drimys brasiliensis* var. *campestris* (St. Hil.) Miers, *Hoehne* 28700. FIG. 2. *Drimys Beccariana* Gibbs, *Brass* 11294. FIG. 3. *Drimys oligandra* A. C. Sm., *Brass* 12975. FIG. 4. *Drimys piperita* Hook. f., *Williams* 754. FIG. 5. *Drimys obovata* A. C. Sm., *Brass* 11295. FIG. 6. *Zygogynum Vieillardii* Baill., *Franc* 1740. FIG. 7. *Bubbia megacarpa* A. C. Sm., *Brass* 10249. FIG. 8. *Pseudowintera axillaris* var. *colorata* (Raoul) A. C. Sm., *Raoul* in 1843.

PLATE II

Drawn with camera lucida from pollen mounted unstained in lactic acid. FIG. 9. *Drimys lanceolata* (Poir.) Baill., *Baker* in 1890. Tetrad showing detail of one pollen grain. \times 1180. FIG. 10. *Zygogynum Vieillardii* Baill., *Franc* 1740. Drawn at a higher focal level than *Fig. 6*, showing finely reticulate exine. \times 1180. FIG. 11. *Belliolum haplopus* (Burtt) A. C. Sm., *Kajewski* 1994. \times 1180. FIG. 12. *Drimys brasiliensis* var. *campestris* (St. Hil.) Miers. *Hoehne* 28700. Outline of tetrad showing protuberances. \times 617. FIG. 13. *The same*. Single grain from dissociated tetrad, showing protuberance from distal germ pore and the structure of proximal facet. \times 1180. FIG. 14. *Asimina angustifolia* A. Gray, *Harbison* 1143. Outline of tetragonal tetrad, showing proximal position of germinal furrows. \times 187. FIG. 15. *The same*. Detail of single grain from dissociated tetrad, showing proximal furrow, \times 480. FIG. 16. *Bubbia monocarpa* A. C. Sm., *Kanehira & Hatusima* 12105. Detail of one grain of tetrad; (a) granular appearance at lower focal level. \times 1180.

PLATE III

Stamens cleared in hot dilute NaOH and mounted unstained in diaphane. Magnification \times 24. FIG. 17. *Drimys confertifolia* Phil., *Bock* 49. FIG. 18. *Drimys grandensis* var. *grandiflora* Hieron., *Archer* 1202. FIG. 19. *Drimys Winteri* var. *chilensis* (DC.) A. Gray, *Werdermann* 73. FIG. 20. *Drimys stipitata* Vickery, *White* 7572. FIG. 21. *Belliolum haplopus* (Burtt) A. C. Sm., *Brass* 2959. FIG. 22. *Bubbia Clemensiae* A. C. Sm., *Clemens* 4596. FIG. 23. *Pseudowintera axillaris* var. *typica* A. C. Sm., *Kirk*. FIG. 24. *Exospermum stipitatum* (Baill.) v. Tiegh., *Vieillard* 2281.

BIOLOGICAL LABORATORIES,
HARVARD UNIVERSITY.